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MONOGRAPHIC STUDIES IN THE GENUS *ELEOCHARIS*<sup>1</sup>

H. K. SVENSON

(Plates 188 to 191)

## INTRODUCTION

It is twenty years since the publication of fragments of C. B. Clarke's monographic work on the *Cyperaceae*. Since that time extensive explorations have been made in the New World where *Eleocharis* has its greatest concentration and where the concept of species within this genus has greatly changed in the last two decades. The nomenclature which Clarke employed is in great need of revision, and, moreover, there has been a lack of critical comparison between Old World and New World forms. Of Clarke's manuscript, nothing has been published except an abstract of species arranged in systematic order and a series of illustrations of selected species from the various genera.

The present work deals with the taxonomy and geographic distribution of *Eleocharis*, a genus of the *Cyperaceae*, consisting of more than a hundred species of aquatic and semi-aquatic plants, inhabiting salt marshes, bogs, and shallow waters of ponds from the tropics to the polar regions of both hemispheres. A genus characteristically without leaves and therefore without the complex foliar variations of leafy plants, it has the photosynthetic activities transferred to the culm. The chief differentiation of species lies in the character of the

<sup>1</sup> A Thesis submitted in partial fulfillment of the Requirements for the degree of Doctor of Philosophy in the Division of Biology, Harvard University, 1928.



achene, and in the study of this the author has constantly employed a binocular dissecting microscope.

For assistance the author is especially indebted to Professor M. L. Fernald, under whose supervision the work was carried out, and to Dr. R. L. Robinson for his kindly advice in many matters, and to the other members of the staff of the Gray Herbarium; to Dr. F. W. Pennell for valuable assistance in the examination of the Muhlenberg, Short and Porter herbaria at the Philadelphia Academy of Sciences and for the loan of material; to Dr. P. A. Munz of Pomona College for the loan of a large collection of *Eleocharis* from the western United States, including the collection of M. E. Jones; to Dr. Gunnar Samuelsson of the Botanical Museum of Stockholm for the loan of South American and West Indian material; to the staff of the New York Botanic Garden, and especially to Dr. J. K. Small; to Dr. M. O. Malte for the loan of material from the Canadian National Museum; and to the National Herbarium at Washington for the loan of South American and Mexican specimens; and to all others who have helped in the loan of specimens and otherwise. The writer has been very fortunate in having at the Gray Herbarium authentic material of most of the species of the Old World, represented by specimens from the collections of Thwaites, Wallich, Hooker, Schweinfurth, Seemann, Mueller, Zollinger, and others, without which a treatment of *Eleocharis* would have been impossible.

From a purely nomenclatorial point of view the genus is of great interest. The name *Eleocharis* given by Robert Brown (1810), is derived from ἔλος (a marsh) and χάρις (grace) and refers to the aquatic habitat. In forming the name Brown did not include the letter "h," represented in Greek only by the rough-breathing mark. Whether *Eleocharis* or *Heleocharis* is the correct spelling has consequently been a source of contention, with continental botanists for the greater part insisting on the "h".<sup>1</sup> C. B. Clarke solved the problem in a very simple manner, by rejecting all combinations under *Heleocharis*, which is not, however, a method that appeals to common sense; and it has been the custom of practically all workers

<sup>1</sup> According to Ascherson & Graebner, Syn, i. 400, footnote 1 (1897), in discussing the similar names *Elodea* and *Helodea*, it arises from "der französischen Unsitte, den griechischen Spiritus asper unbeachtet zu lassen." Yet, withal, Ascherson & Graebner, in citing the derivation of *Eleocharis* (l. c. ii. 289, footnote 1) omit the initial aspirate. Sprague, Kew Bull. Misc. Inf. 1928: 352 (1928) upholds the spelling *Eleocharis* as required by the International Rules of Nomenclature, and his remarks under *Rynchospora* (l. c. 360) are apropos.



to follow the *Index Kewensis* in treating the matter as merely a trivial variation in orthography. In the present paper the variation in the initial letter has not been considered as worthy of differentiation in citing synonymy. However, *Heleocharis* as a name is unjustifiable for several reasons. First, we have no right under the rules to change the original spelling; second, in combining two Greek words into so-called Latin nomenclature, a new language is formed which is not rigorously subject to previous usage; and finally, the name *Heleocharis* tends to be confused with names compounded from "helios" the sun. Into this error Lindley<sup>1</sup> drifted in an unfortunate attempt to correct the name, and others following him have, likewise, erroneously written "*Heliocharis*."

But little is to be gained by an extended review of the classification of *Eleocharis*. Practically all classifications have been based upon arbitrary characters, and are purely artificial. The author has divided the genus into eleven series which he believes to represent natural groups. Under each series are cited the commoner species belonging to it, so that, provided the specimen in hand has mature fruit, there should be little difficulty in determining the affinities of the plant. Robert Brown, Prod. 224 (1810), set apart *Eleocharis* from *Scirpus* and characterized it as follows:

*Squamae* undique imbricatae, conformis: vix ullae steriles. *Setae* hypogynae (4–12) denticulatae, raro nullae. *Stylus* 2–3-fidus, basi dilatata cum ovario articulata. *Nux* saepius lenticularis, basi dilatata indurata styli coronata.

It is, accordingly, to be separated from *Scirpus* on the basis of monocephalic inflorescence without bracts, i. e., "nuda," and an "indurated" style-base which is "dilated" and "articulated" with the ovary. This description applies very well to *E. palustris*, which has generally been taken as typifying the genus, but as in other genera of the *Cyperaceae*, difficulty has arisen in limitation of the description to a natural group. Especially has this been true of the series *Pauciflorae* represented by *E. pauciflora*, *E. parvula*, and *E. rostellata*, the members still being treated by European and some American botanists as either *Scirpus* or *Eleocharis* (*Heleocharis*).

<sup>1</sup> Lindl. Syn. Brit. Fl. 280 (1829) and in succeeding editions. The name is still further complicated by the spelling *Elaeocharis* employed by Ledebour and Schur, arising perhaps from a misconception of the derivation. Also Schultes, Mant. ii. 2 (1824) apparently misread *Heleophila* for *Heleophylax* Lestib. Essai Cyp. 41 (1819) (which seems to refer to *Scirpus validus*, etc.) and substituted the name *Heleogiton* ("character ut in *Heleochari*. Semen nudum") because of the pre-existing *Heliophila*.



However, it seems clear, as it did to Palla<sup>1</sup> on the basis of anatomical investigation, that we are dealing with true *Eleocharis*, for the style-base, though small, is clearly and sharply different in texture from the remainder of the achene (although under insufficient magnification they may appear homogeneous) and is invariably thicker at its junction with the body of the achene than with the base of the style; therefore, it may be interpreted as both "dilated" and "articulated." It is otherwise in the monocephalic *Scirpus Clintonii* and *S. planifolius* of eastern North America, which are related to *Scirpus hudsonianus* (Michx.) Fernald<sup>2</sup> (*Eriophorum alpinum* L.). These have the lowest scale extended as a bract and the soft granular texture of the achene associated with *Scirpus* and *Eriophorum*. Palla's anatomical work undoubtedly paves the way for an understanding of the natural genera under the *Cyperaceae*. However, his separation of *Scirpus* into eight genera:—*Dichostylis* (various species of *Cyperus* and *Fimbristylis*), *Trichophorum*<sup>3</sup> (*S. hudsonianus* Fernald, and allied species), *Scirpus* (*S. cyperinus* and allies), *Holoschoenus* (*S. Holoschoenus*), *Blysmus* (*S. rufus* and *S. Caricis*), *Schoenoplectus* (*S. americanus* and allies), *Heleocharis* and *Isolepis* (*S. carinatus* A. Gray and allies)—increases the already unwieldy number in the *Cyperaceae*; and most of them will probably continue to be treated as sections of *Scirpus*. Palla's treatment has, however, been followed by Schinz & Keller. A great contribution to the knowledge of the *Cyperaceae* has been made by Nees ab Esenbeck,<sup>4</sup> although he split the family into innumerable genera too finely drawn to be accepted at the present time. Several of these genera, i. e., *Chaetocyperus*, *Limnochloa*, *Scirpidium*, *Eleogenus* and *Eleocharis* are now generally included under *Eleocharis*.

In his classic observations on the homology of floral parts in the

<sup>1</sup> Palla, Zur Kenntniss der Gattung "Scirpus," Engler, Bot. Jahrb. x. 299 (1889).

<sup>2</sup> Fernald, RHODORA, viii. 161 (1906); for detailed discussion see Fernald RHODORA, vii. 131, 132 (1905).

<sup>3</sup> *Trichophorum*, as interpreted by Palla, l. c. (1889) and Bot. Zeit. liv. Ab. 1: 146 (1896), consisted of *Eriophorum alpinum* L. (*Scirpus hudsonianus* Fernald), *S. caespitosus* L. and *S. alpinus* Schleich., but did not include *S. (Eleocharis) pauciflorus* Lightf. as Richter erroneously intimated when he listed *Trichophorum pauciflorum* Palla as a synonym in *Plantae Europaeae*, 139 (1890). Palla, l. c. states that such a combination had never been made. *Trichophorum* was first separated as a genus by Persoon, Syn. i. 69 (1805), a "genus intermedium inter Scirpium et Eriophorum," on the basis of the elongated bristles, and comprised *S. alpinus* and *S. cyperinus*.

<sup>4</sup> Especially Nees, *Cyperaceae* in Wight, Contrib. Bot. Ind. (1834); *Linnaea*, ix. 273-306 (1834); and in Martius, Fl. Bras. ii. (1842).



*Cyperaceae*, Nees, *Linnaea*, ix. 281 (1834) wrote: "the pistil consists normally of three carpels, keeled, valvately united, and grown together inwardly, the angles alternating with the inner stamens. From the ovules of these carpels only one develops. Not rarely a carpel is lacking, most generally the one turned toward the axis. The fruit then becomes lenticular or plano-convex with a more convex outer face. The style is more or less 2-3 parted, and the number of these partitions denotes the form of the fruit, whether triangular or lenticular" [translation mine].

Recent subdivisions of *Eleocharis*<sup>1</sup> have been largely based on the number of style-parts (2 or 3) and on the concomitant flattened or triangular achene. However, series of forms can be demonstrated in wholly different groups showing a transition from triangular to lenticular achenes.<sup>2</sup> This criterion, therefore, cannot in itself be maintained as a basis for the separation of sections or subgenera within *Eleocharis*. However, where such a transitional series exists, it may be inferred that species with triangular achenes are, other things being equal, phylogenetically older than those with plano-convex or lenticular achenes. *E. elongata* (confined to Florida) is the only member of the series *Mutatae* having triangular achenes, and it is also the most distinctly aquatic. Its close relatives, *E. Robbinsii* and *E. plicarhachis*, in their occasionally triangular achenes and the persistently triangular base of the style, show clearly the transition. A similar series may be found in the *Pauciflorae*. Plowman, *Ann. Bot.* xx. 25 (1906), on the basis of anatomical studies came to the conclusion that "*Eleocharis* is apparently a long-established and much reduced limicolous genus from near the common origin of the order." By him the *Monocotyledon* prototype is hypothetically considered as a large-leaved aquatic which was driven by drouth or flooding "to the dry banks, or carried into humus bogs and salt marshes," thus deriving on the one hand the rhizomatous genus *Carex* and on the other hand the tuberous genus *Cyperus*. At the same time came a reduction of fundamental tissue and changes in the stelar structure, notably the formation of amphivasal bundles.

Bristles and stamens are likewise exceedingly variable throughout the genus. The normal perianth of six bristles—of extreme import-

<sup>1</sup> Cf. C. B. Clarke, *Kew Bull. Add. Ser.* viii. 105 (1908).

<sup>2</sup> Such a characteristic is not confined to *Eleocharis* but occurs also in *Scirpus* and in the *Polygonaceae* (*Polygonum*).



ance in classification under the artificial Linnean system, even as to the delineation of genera (cf. *Isolepis* R. Br.)—is often reduced, or may be entirely absent.

The number of bristles may be exceedingly constant in some species, and their lack a situation of great rarity, as in *E. capitata* (*E. tenuis*); or the bristles may be commonly either present or absent, as in *E. Engelmanni* and *E. caribaea*; or they may be of a constant reduced size. In all cases the degree of variation is a character confined to the individual species. The bristles are very constant in their texture within a species, and this texture may prove to be one of the most valuable means of identification. In the case of the lenticular achene five bristles are normally found on the outer or abaxial face of the achene—the face which is enveloped by the subtending scale—and the sixth bristle, which belongs to the inner series, is found at the middle of the inner or axial face. The three stamens also occur on the outer face, one of them median, one at each margin of the achene. Where more than six bristles are present, the supernumerary bristles will be found to result from a branching of the bristle on the inner face. This is commonly bifid, resulting in a total of seven bristles, or as in *E. sphacelata*, may be divided into as many as four branches, giving a total of nine bristles. Due to the pressure of time the writer has not had opportunity to study in a detailed way the anatomy of the achene, especially with reference to variation of carpels in the lenticular achene as compared with the triangular achene. Is the lenticular achene induced by crowding in the spikelet, or by the more advantageous position taken up by the stamens toward the periphery of the spikelet?

Two monographs dealing with the North American species of *Eleocharis* have appeared; the first of these by Torrey<sup>1</sup> and the more recent by Britton.<sup>2</sup> The volumes by Roemer & Schultes (1817), Kunth (1837) and Steudel (1855) are mainly compilations, and the work of Boeckeler is to a large extent merely a description of plants without critical comparison between the species. C. B. Clarke's monograph of the *Cyperaceae* has never been published but his classification of species<sup>3</sup> and illustrations<sup>4</sup> were issued after his death.

The bibliography has been assembled (at the end of this paper)

<sup>1</sup> Torr. Ann. Lyc. Nat. Hist. N. Y. iii. 296–316 (1836).

<sup>2</sup> Britt. Journ. N. Y. Micr. Soc. v. no. 4: 95–111 (1889).

<sup>3</sup> Clarke, Kew Bull. Add. Ser. viii. (1908).

<sup>4</sup> Clarke, Illustr. Cyperac. London. (1909).



from three points of view: (1) a citation of recent literature dealing with *Eleocharis*; (2) a citation of a few fundamental systematic treatments; (3) the assembling of scattered publications of C. B. Clarke dealing with *Eleocharis*.

In the problem of dealing with entities below the specific rank it is the policy to treat as *varieties* those which show a definite geographic segregation; and as *forms* those without geographical segregation.

The following abbreviations for herbaria are used:

CANADIAN NATIONAL MUSEUM—(C.)

UNITED STATES NATIONAL MUSEUM—(U.S.)

NEW ENGLAND BOTANICAL CLUB—(N.E.B.C.)

NEW YORK BOTANIC GARDEN—(N.Y.)

POMONA COLLEGE—(P.)

PHILADELPHIA ACADEMY OF SCIENCES—(Ph.)

BOTANICAL MUSEUM, STOCKHOLM—(S.)

GRAY HERBARIUM—(G.)

Unless otherwise noted, specimens are in the Gray Herbarium.<sup>1</sup>

## ELEOCHARIS

### PRELIMINARY CONSPECTUS OF THE GENUS

Series 1. MUTATAE *Limnochloa* Nees in Wight, Contr. Bot. Ind. 71 (1834) and Linnaea, ix. 294 (1834), not Lestib. Essai Cyp. 41 (1819) nor Reichb. Fl. Germ. Excurs. i. 78 (1830). *Eleocharis* § *Limnochloa* Torr. Ann. Lyc. Nat. Hist. N. Y. iii. 296 (1836). *Eleocharis* Subgen. *Limnochloa* C. B. Clarke, Kew Bull. Add. Ser. viii. 105 (1908). Mostly coarse plants with swollen culms which are often as thick as the spikelets. Scales not keeled or only obscurely so, usually indurated, yellow, sometimes with a purple margin. Achenes lenticular (triangular only in some slender New World species), the bristles usually coarse. Style elongated, flat, 2-fid or 3-fid. *E. interstincta*, *E. dulcis* (*plantaginea*), *E. mutata*, *E. fistulosa*, *E. Robbinsii*, *E. cellulosa*, etc.

Series 2. PAUCIFLORAE. *Scirpus* C. B. Clarke, Kew Bull. Add. Ser. viii. 111 (1908) in part. Style-base confluent with the apex of the achene (in some Andean species forming a ridge at the

<sup>1</sup> This paper on *Eleocharis* follows directly upon the work by Professor M. L. Fernald and Miss A. E. Brackett, The Representatives of *Eleocharis palustris* in North America, RHODORA xxxi. 57-77 (1929) and Contributions from the Gray Herbarium, no. lxxxiii. It has, therefore, seemed unnecessary to repeat the treatment of the North American species considered by them.

I have just received, from Professor Chermeson, too late to be incorporated in the present paper, a number of specimens of *Eleocharis* from Madagascar. These I hope to include in a succeeding paper. There has also just come to me the excellent and well-illustrated paper on *Eleocharis* by Barros, dealing in great detail with the genus in Argentina. This I must also leave for future consideration.



junction of the style-base and the body of the achene). Achenes greenish or tawny, trigonous, usually reticulate under high magnification. Style 3-fid. *E. pauciflora*, *E. parvula* (*Scirpus nanus*), *E. rostellata*, *E. albibracteata*, *E. Brehmeriana*, etc.

Series 3. ACICULARES. *Eleocharis* Subgen. *Eu-eleocharis* Sec. *Aciculares* C. B. Clarke, l. c. 105. Achenes obscurely trigonous or terete, elongated, with longitudinal ridges separated by numerous trabeculae. Lowest scale fertile. Style 3-fid. *E. acicularis*, *E. cancellata*, *E. Wolfii*, *E. bonariensis*, etc.

Series 4. OVATAE. *Eleocharis* Subgen. *Eleogenus* b. *Capitatae* C. B. Clarke l. c. 105, in part. Style-base compressed, lamelliform; achenes biconvex, glistening-brown when mature, under magnification smooth. Style 2-fid. Cespitose annuals. *E. ovata*, *E. obtusa*, *E. Engelmanni*, *E. diandra*, *E. lanceolata*.

Series 5. MACULOSAE. *Eleocharis* Subgen. *Eleogenus* C. B. Clarke l. c. 105, in part. Style-base conical or depressed, not lamelliform. Achenes biconvex, black to reddish-brown or olive, the surface smooth or minutely wrinkled under magnification. Style 2-fid.

Sub-series: OCREATAE. Perennial; stoloniferous. Sheaths scarious at the apex. Achenes black to reddish-brown or olivaceous; pericarp marcescent, often slightly wrinkled under magnification. *E. flaccida*, *E. olivacea*, *E. maculosa*, *E. Sellowiana*, *E. debilis*, etc.

Sub-series: RIGIDAE. Annual; without stolons. Sheaths firm at apex. Achenes black or purplish; pericarp not marcescent. *E. atropurpurea*, *E. caribaea*, *E. praticola*, etc.

Series 6. PALUSTRIFORMES. Style-base spongy, beak-like, rarely depressed. Achenes bright-yellow to tawny or olivaceous, biconvex or trigonous, smooth to alveolate. Plants usually stoloniferous, with strict, elongated, sometimes spongy culms.

Sub-series: PALUSTRES. *Eleocharis* Subgen. *Eleogenus* c. *Palustres* C. B. Clarke, l. c. 105. Style 2-fid. Upper sheaths oblique at the summit. Achenes lenticular (biconvex), yellow or brown, smooth under magnification. *E. palustris*, *E. uniglumis*, *E. mamillata*, etc.

Sub-series: TRUNCATAE. *Eleocharis* Subgen. *Eu-eleocharis* Sect. *Leiocarpeae* c. *Montanae* C. B. Clarke l. c. 106, in part. Styles 3-fid. Upper sheaths truncate, indurated, with a small apiculate projection. Achenes trigonous (in *E. nodulosa* and *E. geniculata* almost or quite lenticular); the surface under magnification alveolate, reticulate or smooth. (In *E. nodulosa* the style is frequently 2-fid.)

Culms not septate, *E. montana*, *E. capitata* (*E. tenuis*), *E. compressa*, *E. nitida*, *E. arenicola*, *E. tricostata*, *E. densa*, *E. Bolanderi*, etc.

Culms septate: *E. nodulosa*, *E. geniculata*.

Note: To this series also belongs *E. fallax* Weatherby.



Series 7. INTERMEDIÆ. Style-base elongated, beak-like; style 2-fid or 3-fid. Achenes elongated, olivaceous, lenticular or obscurely 3-angled; under magnification striate or minutely reticulate. Cespitose plants with weak culms and acuminate spikelets. *E. intermedia*, *E. Macounii*, *E. carniolica*, *E. afflata*, *E. Widgrenii*, etc.

Series 8. TENUISSIMÆ. Plants for the most part dwarf, tufted, and with capillary culms. Achenes small (0.4–1 mm. long), sharply or obscurely trigonous (in *E. savannarum* almost lenticular). Spikelets often distichous. Achenes present at the culm-bases in many species. Style 3-fid.

Sub-series: CHÆTARIÆ. *Eleocharis* Subgen. *Eu-eleocharis* Sect. *Chaetariæ* C. B. Clarke, l. c. 106, in part. Achenes coarsely reticulate, *i. e.* cancellate. *E. retroflexa*, *E. arenaria*, *E. savannarum*, etc.

Sub-series: LEIOCARPEÆ. *Eleocharis* Subgen. *Eu-eleocharis* Sect. *Leiocarpeæ* C. B. Clarke, l. c. 106, in part. Achenes smooth or very finely reticulate under magnification.

Spikelets not distichous or only obscurely so. *E. microcarpa*, *E. nana*, *E. Torreyana*, *E. nigrescens*, etc.

Spikelets clearly distichous: *E. Baldwinii*, *E. oligantha*, *E. minima*, *E. urceolata*.

Series 9. SULCATAÆ. *Eleocharis* Subgen. *Eu-eleocharis* Sect. *Leiocarpeæ* b. *Sulcatae* C. B. Clarke, l. c. 106, in part. Achenes white, sharply or obscurely trigonous, usually exceeding 1 mm. in length. Culms usually strict and coarser than in the preceding section. Style 3-fid. *E. sulcata*, *E. pachystyla*, *E. pachycarpa*, *E. albida*, *E. bermudiana*, etc.

Series 10. MELANOCARPEÆ. Achenes black, smooth, sharply trigonous. *E. melanocarpa*.

Series 11. TUBERCULOSÆ. *Eleocharis* Subgen. *Eu-eleocharis* Sect. *Chaetariæ* C. B. Clarke, l. c. 106, in part. Achenes obscurely trigonous; style-base enlarged and mitriform, sometimes equalling the body of the achene in size. The American species with achenes deeply cancellate. *E. tuberculosa*, *E. simplex*, *E. tetraquetra*, *E. Wichurii*.

### Series MUTATAE

(Plate 188)

a. Culms septate. . . . b.

b. Surface of achene reticulate, often with conspicuous longitudinal ridges. . . . c.

c. Surface of the orbicular achene with inconspicuous hexagonal or square cells. . . . d.

d. Spikelets 4–5 mm. in diameter; scales gray; bristles 6–7

13. *E. dulcis*.

d. Spikelets 5–8 mm. in diameter; scales light-brown; bristles

7–9. . . . . 14. *E. sphacelata*.



- c. Surface of achene with transverse linear cells. . . . e.
  - e. Septa approximate below the spikelet; bristles coarse, exceeding the achene. . . . . 1. *E. interstincta*.
  - e. Septa not approximate; bristles poorly developed; achene nearly smooth. . . . . 2. *E. equisetoides*.
- b. Surface of the elliptic achene merely punctulate; culms slender
  - 15. *E. equisetina*.
- a. Culms not septate. . . . f.
  - f. Culms angled; bristles toothed. . . . g.
    - g. Culms coarse (2–5 mm. in diameter). . . . h.
      - h. Culms 4-angled; achene constricted below the summit into a neck about  $\frac{1}{4}$  the width of the achene. . . . 3. *E. quadrangulata*.
      - h. Culms 3-angled. . . . i.
        - i. Achene constricted below the summit into a neck about  $\frac{1}{2}$  the width of the achene. . . . . 7. *E. fistulosa*.
        - i. Achene not constricted, but gradually prolonged into a cellular beak. . . . j.
          - j. Achene dark-brown, with obscure narrowly linear cells
            - 5. *E. spiralis*.
          - j. Achene yellowish, with conspicuous quadrangular cells
            - 4. *E. mutata*.
  - g. Culms slender (1–2 mm. in diameter). . . . k.
    - k. Achene 1 mm. long, trigonous; culms often floating. . . 9. *E. elongata*.
    - k. Achene exceeding 1.5 mm. in length, lenticular (rarely trigonous in *E. Robbinsii* and *E. plicarhachis*). . . . l.
      - l. Surfaces of achene with deep-pitted hexagonal cells; spikelets elongate, with spreading scales. . 10. *E. philippinensis*.
      - l. Surfaces of achene with transverse quadrangular cells. . . m.
        - m. Achene elongate (about 4 mm. in length); spikelet appearing like a continuation of the sharply triangular culm. . . . . 8. *E. Robbinsii*.
        - m. Achene orbicular, 2–3 mm. long; spikelet contrasting with the obscurely triangular or terete culm. . . . n.
          - n. Culms dull, rigid; faces of achene with 20–25 rows of linear-quadrangular cells; base of style  $\frac{1}{2}$ – $\frac{3}{4}$  the width of the achene. . 11. *E. variegata* var. *laxiflora*.
          - n. Culms shiny, soft; faces of achene with 12–15 rows of quadrangular cells; base of style  $\frac{1}{3}$  the width of the achene. . . . . 12. *E. plicarhachis*.
  - f. Culms terete; achene prolonged into a cellular beak; bristles without teeth. . . . . 6. *E. cellulosa*.

1. *E. INTERSTINCTA* (Vahl) R. & S. FIG. 2. Culms terete, 4–10 dm. high, about 5 mm. thick, septate; the septations becoming approximate below the spikelet: caudex short; roots coarse, light-brown or reddish-brown: sheaths membranous, pointed at the summit; the basal sheaths sometimes free and elongated: style 2- or 3-fid: stamens 3: spikelets cylindric, 1.5–4 cm. long, many-flowered: scales in several ranks, oblong, often acute, striate, straw-colored or grayish, with a scarious margin: achenes rough, 2 mm. long (excluding the style-base), yellow or gray, with prominent transverse rectangular cells often forming longitudinal ribs, and a pronounced annular thickening at the summit: style-base dark-brown: bristles 6, exceeding the achene, stout, flattened, with coarse teeth.—Syst. ii. 149 (1817); Britton, Journ. N. Y. Micr. Soc. v. 97 (1889) excl. *E. equisetoides*



and syn. in part; C. B. Clarke in Urb. Symb. Ant. ii. 60 (1900) in part, Ill. Cyp. t. 33, figs. 6–9 (1909). *Scirpus plantagineus* Swartz, Fl. Ind. Occ. i. 123 (1797), excl. syn.; and of many later auth., not of Retz. *S. interstinctus* Vahl, Enum. ii. 251 (1805). *Limnochloa articulata* Lindl. & Nees in Mart. Fl. Bras. ii.<sup>1</sup> 100 (1842).<sup>1</sup> *E. articulata* Kunth, En. ii. 157 (1837). *E. septata* Miq. Linnaea, xvii. 58 (1843). *E. articulata* Steud. Cyp. 81 (1855). *E. plantaginea* Boeckl. Linnaea, xxxvi. 474 (1869–1870) and Cyp. Nov. ii. 14 (1890), as applied to the American plant. *S. polygamus* Wright mss. ex Boeckl. Flora, lxiv. 78 (1881).—In shallow water, Texas, Bermuda Islands, West Indies, and northern and central South America. TEXAS: (W. Tex. to El Paso) C. Wright 707; Del Rio, Neally 112 (N.Y.). BERMUDA: Robinson 102; Moore 3010; Collins 169; Harshberger in 1905. CUBA: C. Wright 710, 3768 (as *S. polygamus*); Combs 431; Prov. Santiago, Pollard & Palmer 305; Isle of Pines, Curtiss 498. GRENADA: Broadway in 1905. JAMAICA: Alexander in 1850 (in part). HAITI: Leonard 3538. COLOMBIA: Santa Marta, H. H. Smith 245; San Antonio, Langlassé 34. BRITISH GUIANA: Georgetown, Hitchcock 16652. DUTCH GUIANA: Hostmann 661; Samuels 508. BRAZIL: Burchell 4159, 2650; Para, Goeldi 1039. BOLIVIA: Lake Rogagua, Rusby 1422.

Vahl first described this plant (as *Scirpus*) from Martfeld's West Indian collection, and characterized it as similar to *Scirpus geniculatus* but with "*isthmi superne approximati, nec remotissimi*," a character which also separates it from the more northern *Eleocharis equisetoides*. In addition, the achene of *E. interstincta* is coarser than in *E. equisetoides*, with deeper pittings and stronger bristles. The Wright plant labeled *S. polygamus* (3768) in the Gray Herbarium is rather immature, with thin culm and elongated spikelets, but is unquestionably *E. interstincta*.<sup>2</sup> The figure in Britton & Brown Ill. Fl. is of *E. equisetoides*.

2. *E. EQUISETOIDES* (Ell.) Torr. FIG. 1. Culms terete, 5–10 dm. high, about 5 mm. thick, prominently septate at intervals of 1–5 cm.; the surface roughened by numerous minute projections: caudex short; roots coarse, reddish brown: sheaths membranous, pointed at the summit; those at the base often free from the culm and greatly elongated: style 2- or 3-fid: stamens 3: spikelets cylindrical, 2–4 cm. long, many-flowered: scales in several ranks, oblong, striate, straw-colored, with an obscure purplish border beneath the scarious margin:

<sup>1</sup> *Eleocharis articulata* Kunth, Enum. ii. 157 (1837) was wrongly ascribed to Nees by Kunth (Flora, ix. 294 (1835) where Nees used the name *Limnochloa articulata* as a *nomen nudum*. The first valid publication of this synonym is in Martius, Flora Brasiliensis, as quoted above.

<sup>2</sup> Boeckeler, Flora, lxiv. 78 (1881) says that this plant is *E. plantaginea* R. Br., forma americana.



achenes nearly smooth, 2–2.5 cm. long (including the style-base), golden-yellow or light-brown, broadly obovate, biconvex, with fine transverse linear-rectangular reticulations: style-base dark-brown: bristles narrow and weak, rarely equalling the achene.—Ann. Lyc. N. Y. iii. 296 (1836). *Scirpus geniculatus* Pursh, Fl. Am. Sept. i. 55 (1814), not L. *S. equisetoides* Ell. Sk. S. Car. i. 79 (1816). *S. obtusus* Willd. in Spreng. Syst. i. 204 (1825), in part. *E. Elliotti* A. Dietr. Sp. Pl. ii. 82 (1833). *E. interstincta* Britton, Journ. N. Y. Micr. Soc. v. 97 (1889), in part; Britton & Brown Ill. Fl. i. 248 (1896), as to fig. not (Vahl) R. & S.—Shallow water, Massachusetts to Florida and Texas, chiefly on the coastal plain, and locally inland to Michigan and Wisconsin. MASSACHUSETTS: Lake Waban, Wellesley, *Morong* in 1883; *Fernald & Wiegand*, Pl. Exs. Gray. 132. RHODE ISLAND: Cumberland, *Olney*; Tippecan Pond, West Greenwich, *Graves & Woodward* in 1920. CONNECTICUT: Long Pond, Thompson, *Weatherby* 4370. NEW YORK: Sag Harbor, L. I., *Cathan & Ferguson* 5829. NEW JERSEY: pond south of Repaupo, *Van Pelt* in 1907. MARYLAND: Salisbury, *Canby* in 1865. SOUTH CAROLINA: Santee Canal, *Ravenel*. GEORGIA: Sumter Co., *Harper* in 1897; Lee Co., between Rift and Chokey, *Harper* 1071. FLORIDA: Eustis, *Nash* 1322. MICHIGAN: Jackson Co., *J. Wright* in 1838; Pleasant Lake, *Hicks* in 1893. ILLINOIS: Chicago (Wolf Lake), *Hill* in 1890 (mixed with *E. quadrangulata*). TEXAS: *C. Wright*. LOUISIANA: *Buckley* in herb. Short (Ph.).

This species can be readily distinguished from *E. interstincta* by the remote articulations below the spikelet and by the roughened character of the culms. The smooth achene is decidedly different. Pursh described *Scirpus geniculatus* from “the sea-shore of Virginia and Carolina”; but, although the Pursh specimens have disappeared, there can be no question as to the identity, for *E. geniculata* is confined to the tropics. The species (*E. equisetoides*) was described by Elliott from specimens collected by Schweinitz near Fayetteville, North Carolina, but was merged with the tropical *E. interstincta* by Clarke.

3. *E. QUADRANGULATA* (Michx.) R. & S. FIG. 4. Culms 4-sided, with sharp angles, coarse, 5–10 dm. high, from a short caudex: roots coarse, gray, often tuber-bearing: sheaths red or brown, membranous, with a loose brown tip, glistening, sometimes prolonged into leaf-like blades: spikelets 2–5 cm. long, cylindric, acute: scales 4-ranked, elliptic, 5 mm. long, 2 mm. wide, rounded or somewhat acute, straw-colored, striate, not keeled: style 2- or 3-fid: stamens 3: achene 2.7–4.2 mm. long including the beak (1 mm. long), narrowly obovate, deep shining-brown, almost smooth, with about 24 rows of transverse linear cells, narrowed at the summit to a neck about one-fourth the width of the achene, broadening again to form the base of



the elongated triangular style: bristles light-brown, equalling the achene, slender and obscurely toothed.—Syst. ii. 155 (1817); Torr. Ann. Lyc. N. Y. iii. 297 (1836); Boeckl. Linnaea, xxxvi. 472 (1869–1870); Fernald, RHODORA, xxvii. 38, t. 149, figs. 1–4 (1905). *Scirpus quadrangulatus* Michx. Fl. Bor.-Am. i. 30 (1803); Elliott, Sk. S. Car. i. 78, t. 3, fig. 2 (1816). *S. marginatus* Muhl. Gram. 28 (1817). *S. albomarginatus* R. & S. Mant. ii. 74 (1824). *E. mutata* Britton & Brown, Ill. Fl. ed. 2, i. 311, fig. 759 (1913), not *S. mutatus* L.—In ponds, often on peaty shores, Massachusetts to southern Ontario, south to Georgia, Louisiana and Texas, chiefly on the coastal plain. MASSACHUSETTS: Lake Waban, Wellesley, *Fernald & Wiegand*, Pl. Exs. Gray. 133. CONNECTICUT: West Pond, North Guilford, *Bartlett* 782. NEW YORK: Duck Lake, Conquest, *Wiegand, Eames & Randolph* 11410; Oneida Lake, *Curtiss* in 1866; Oswego Co., Paddy Lake, South Scriba, *W. W. Rowlee* in 1906. NEW JERSEY: Cape May, *Van Pelt* in 1906; Johnson's Pond, Dennisville, *C. F. Parker* in 1866; Swartswood Pond, Sussex Co., *Porter* in 1878. PENNSYLVANIA: Presque Isle, *Porter* in 1868. DELAWARE: *Canby*; Townsend, *Commons* in 1868. DISTRICT OF COLUMBIA: near Washington, *L. F. Ward* in 1884. VIRGINIA: Princess Anne Co., Salt Pond, *Randolph* 470; Cape Henry, *Randolph* 334; Chickahominy River, Wilcox Neck, *Grimes* 4125; Franklin, Southampton Co., *Heller* 1149. SOUTH CAROLINA: Santee Canal, *Ravenel*. GEORGIA: Chatham Co., near Savannah, *Harper* 1835. ONTARIO: Lambton Co., Sarnia Bay, *C. K. Dodge* in 1894. MICHIGAN: Ingham Co., Pine Lake *Thurber* in 1860. OHIO: Portage Co., E. Twin Lake, *Webb* in 1915. ILLINOIS: Chicago (Wolf Lake), *E. J. Hill* 90 in 1890 (in part). MISSOURI: Newton Co., *Bush* 370; St. Louis, *Drummond*. OKLAHOMA: Mill Pond, Sapulpa, *Bush* 631. LOUISIANA: *Carpenter*. TEXAS: Hempstead, *E. Hall* 695; E. Texas, *C. Wright*.

Originally described by Michaux from Carolina; but Muhlenberg independently described it (1817) as *S. marginatus*, a name antedated by *S. marginatus* Thunberg, Prod. Fl. Cap. 17 (1794) and therefore changed by Roemer and Schultes (1824) to *S. albomarginatus*. Britton has considered *E. quadrangulata* as only a form of *E. mutata* (L.) R. & S., but Fernald<sup>1</sup> has shown that it is quite distinct from *E. mutata*, in the constricted base of the tubercle and the consistently 4-angled culm. Torrey (l. c.) observed also the strong resemblance to *Scirpus acutangulus* Roxb.

4. *E. MUTATA* (L.) R. & S. FIG. 8. Culms sharply triangular,

<sup>1</sup> Fernald, M. L. The Validity of *Eleocharis quadrangulata*, RHODORA xxvii. 37–40, t. 149 (1925). Three species of America have recently been passing under the name *E. mutata*: namely *E. quadrangulata*, *E. mutata*, and *E. fistulosa*. *E. fistulosa* differs from *E. quadrangulata* in the 3-angled culm and smaller achenes with characteristic markings.



coarse, 4–10 dm. high, from a short caudex; roots very numerous, fibrous gray or brown: sheaths straw-colored or light brown, membranous, pointed at the summit, often elongated: spikelets 1.5–5 cm. long, cylindric, usually obtuse: scales many-ranked, straw-colored, thin, orbicular to obovate, with broad membranous sides, and an erose upper margin, often slightly keeled: style 3-fid: stamens 3: achene 1.7–2.3 mm. long (including the style-base), elliptical or obovate, shining, rather smooth, yellow to brown, with about 24 rows of shallow, transversely linear cells with their margins often slightly raised, surmounted at the summit by an annular thickening which merges gradually into the short style-base: bristles 6, irregular, equalling the achene, lustrous-brown, with coarse but soft teeth.—Syst. ii. 155 (1817); Kunth, Enum. ii. 154 (1837); C. B. Clarke in Urb. Symb. Ant. ii. 61 (1900), excl. syn.; Britton & Brown, Ill. Fl. ed. 2, i. 311 (1913), in part; Fernald, RHODORA, xxvii. 39, t. 149, figs. 11–14 (1925). *Scirpus mutatus* L. Amoen. Acad. v. 391 (1759); Sp. Pl. ed. 2, i. 71 (1762); Vahl. Enum. ii. 252 (1805); Griseb. Fl. Brit. W. I. 571 (1864). *Limnochloa mutata* Nees, Linnaea, ix. 294 (1835). *E. scariosa* Steud. Cyp. 80 (1855). *E. spiralis* Boeckl. Linnaea, xxxvi. 473 (1869–1870), as to American plant.—West Indies, Central America, and northern South America. JAMAICA: *Harris* 12310. PORTO RICO: *Sintenis*. 4942 (*H. spiralis* det. Boeckl.). ST. CROIX: *Ricksecker* 210. ST. JAN: *Eggers* in 1877. VIRGIN ISLANDS: *Fishlock* 316. GRENADA: *Broadway* 1794. PANAMA: Canal Zone, *Pittier* 6775. VENEZUELA: vic. Maracaibo, *Pittier* 10685; El Limon near Maracay, *Pittier* 10116; vic. Cristobal Colon, *Broadway* 580. COLOMBIA: Dept. El Valle, Buenaventura, *Killip* 11744. GALAPAGOS ISLANDS: Albemarle Is., *Snodgrass & Heller* 261;<sup>1</sup> *Stewart* 1081. GUADELOUPE: *Duss* 3441. BRITISH GUIANA: Pomeroon District, *De La Cruz* 941. FRENCH GUIANA: *Broadway* 203. BRAZIL: *Martius* 229.<sup>2</sup> PARAGUAY: Cerros de Tobaty, *Hassler* 6414. (GUATEMALA: *Tuerckheim* 1283. The specimen is very young. It may belong with this species.)

The plant was originally described from Jamaica by Elmgren, a student of Linnaeus. It differs from *E. quadrangulata* in characters previously mentioned under that species, and also in the orbicular scales. It seems most closely related to *E. spiralis* of the Old World, to which it was referred by Boeckeler. The scales of *E. spiralis* are firmer, more sharply truncate, and the spikelets shorter and thicker

<sup>1</sup> Fernald RHODORA, xxvii. 39, and t. 149, fig. 11 (1925) considers this specimen as not characteristic, since the apex of the achene is somewhat constricted, and that it might be worthy of separation when more collections were available. The material is rather fragmentary. The achenes are smaller than the average but have the cellular structure and the same type of bristle as in typical *E. mutata*. The other collection (*Stewart* 1081) from Albemarle Island is typical *E. mutata*.

<sup>2</sup> *E. scariosa* Steud. was based on Nees 229, deriving its name from the scarious development of the lowest sheaths, which, however, is a common occurrence in the group to which *E. mutata* belongs.



than in *E. mutata*. The shiny achenes resemble those of *E. mutata* but are smoother, with finer markings and a deep chocolate-brown color. The bristles of the Borneo plant<sup>1</sup> are more slender and have irregularly scattered teeth.

In the spongy texture of the achene and the character of the beak, *E. mutata*, *E. spiralis* and *E. cellulosa* seem to form a group of closely related species. C. B. Clarke (Urb. Symb. Ant. ii. 61 (1900)) considered *E. mutata* a species quite different from *E. spiralis* R. Br., which grows in southeastern Asia, and perhaps best joined specifically with *E. fistulosa* Schultes, a species growing in both the Old and the New Worlds.

5. *E. SPIRALIS* (Rottb.) R. & S. FIG. 12. Culms sharply triangular, 4–8 dm. high, 2–3 mm. wide: spikelets cylindrical, 1.5–2.5 cm. long, 5–6 mm. wide, obtuse: scales cuneate, 3 mm. long, light-brown, striate, firm; the truncate upper edge with a hyaline margin: style 3-fid: stamens 3: achene elliptic, 2–2.4 mm. long (including the beak), shining, dark-brown, lenticular, with about 20 rows of transverse linear-quadrangular cells, with light-brown beak: bristles 6, brown, equaling the body of the achene, with both antrorse and retrorse teeth.—Syst. ii. 155 (1817); Boeckl. Linnaea, xxxvi. 473 (1869–1870), in part; Benth. & Muell. Fl. Austr. vii. 292 (1878), in part; C. B. Clarke in Hook. f. Fl. Brit. Ind. vi. 627 (1893), in Durand & Schinz, Consp. Fl. Afr. v. 601 (1895), and Ill. Cyp. t. xxxv. figs. 5–7 (1908). *Scirpus spiralis* Rottb. Desc. et Ic. 45, t. xv. fig. 1 (1773); Roxb. Fl. Ind. (ed. Wall.) 215 (1820). *Limnochloa spiralis* Nees in Wight, Contrib. Bot. Ind. 114 (1834).—According to C. B. Clarke, the species occurs in southern India, Ceylon and Mauritius. BRITISH NORTH BORNEO: Jesselton, *Clemens* 9716 (distributed as *E. variegata*), is the only specimen of the species in the Gray Herbarium.

Very closely related to *E. cellulosa* and *E. mutata*<sup>2</sup> of the New World, which it resembles in the peculiar glassy surface of the achene, stout beak and short scales; but *E. spiralis* differs from *E. cellulosa* in the elongated linear cells of the achene, the less spongy beak, toothed bristles and truncate scales, and in the thicker spikelet. The description is largely based upon *Clemens* 9716 which lacks rootstocks. First described by Rottböll from specimens sent to him by Koenig from Malabar (India), the name being derived from the spiral arrangement of the scales.

<sup>1</sup> There is no authentic material of *E. spiralis* in the Gray Herbarium, but *Clemens* 9716, from Borneo (distributed as *E. variegata*), agrees with Clarke's illustration of *E. spiralis* (C. B. Clarke, Ill. Cyp. t. xxxv. figs. 5–7 (1909)) and with descriptions.

<sup>2</sup> See discussion under *E. mutata*.

(To be continued.)